TWO FOSSIL FLOWERS OF *TRICHILIA* (MELIACEAE) IN DOMINICAN AMBER

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ABSTRACT

Mid-Tertiary amber from the Caribbean island of Hispaniola has yielded flowers of several eudicot species characteristic of tropical and subtropical forests of that time period. We here describe as new species two recently discovered Dominican amber flowers, which we assign to *Trichilia*, the largest genus of Meliaceae in the neotropics (Pennington et al. 1981). Both flowers possess features that frequently occur in the genus, such as a dish- or cup-shaped calyx, spreading or recurved petals, and completely fused filaments forming a cylindrical or cyathiform tube that bears acute or apiculate lobes alternating with the anthers on the rim. One flower is complete, with pistil and anthers present, while on the second, the pistil and all but one anther have been damaged or removed by insect predation. The one remaining anther is malformed and non-functional; the filament tube appears to be filled with debris left by the putative insect herbivore. The two fossils differ in their calyx shape and pubescence, corolla pubescence, and filament tube shape, and are described as the new species **Trichilia glaesaria** and **Trichilia antiqua.**

RESUMEN

El ámbar del Terciario medio de la isla caribeña de la Hispaniola ha aportado flores de varias especies de eudicotiledóneas características de bosques tropicales y subtropicales de aquel periodo de tiempo. Describimos aquí como nuevas especies dos flores descubiertas recientemente en el ámbar dominicano, que asignamos a *Trichilia*, el mayor género de Meliaceae en el neotrópico (Pennington et al. 1981). Ambas flores tienen características que ocurren frecuentemente en el género, tales como un cáliz en forma de plato o taza, petalos extendidos o recurvados, y filamentos completamente fusionados formando un tubo cilíndrico o ciatiforme que tiene lóbulos agudos o apiculados alternando con las anteras en el borde. Una flor está completa, con pistilo y anteras presentes, pero en la segunda, el pistilo y el resto excepto una antera han sido dañados o quitados por predación de insectos. La única antera que queda está mal formada y no es funcional; el tubo de los filamentos parece estar lleno de restos dejados por el putativo insecto herbívoro. Los dos fósiles difieren en la forma del cáliz y su pubescencia, pubescencia de la corola, y forma del tubo de los filamentos, y se describen como las nuevas especies **Trichilia glaesaria** y **Trichilia antiqua.**

INTRODUCTION

A reconstruction of the Late Oligocene/Early Miocene tropical forests of Hispaniola was provided by Poinar & Poinar (1999), based on fossil plant and animal remains in amber derived from resin of the arborescent legume *Hymenaea protera*. Novel taxa recently described from flowers found in these deposits include species of *Licania* (Chrysobalanaceae) (Poinar et al. 2008a, revised by Chambers & Poinar 2010), *Persea* (Lauraceae) (Chambers et al. 2011), and *Trochanthera* (possibly Moraceae) (Poinar et al. 2008b). The flowers newly reported here are referable to Meliaceae, a large and commercially important family found throughout the Old and New World tropics and subtropics, but also penetrating into temperate zones. Although on one flower the pistil, one petal, and most of the anthers are missing, very likely through the predation of an insect, we believe the flower structure of both fossils, in particular the characteristic filament tube with sharply pointed lobes between the anthers, point to their placement in *Trichilia* P. Browne. We here propose their description as the new species *Trichilia glaesaria* and *Trichilia antiqua*.

MATERIALS AND METHODS

The fossils originated from mines in the Cordillera Septentrional of the Dominican Republic, between the cities of Puerto Plata and Santiago. Dating of these amber deposits is controversial, with a youngest proposed age of 20–15 mybp, based on foraminifera (Iturralde-Vinent & McPhee 1996) and an oldest of 45–30 mybp based on coccoliths (Cêpek in Schlee 1999). Most of the amber is secondarily deposited in turbiditic sandstones of the Upper Eocene to Lower Miocene Mamey Group (Draper et al. 1994).

DESCRIPTIONS

Trichilia glaesaria K.L. Chambers, Poinar, & A.E. Brown, sp. nov. (**Figs. 1–2**). TYPE: HISPANIOLA. DOMINICAN REPUBLIC: amber mine in the northern mountain range (Cordillera Septentrional), 1995, *unknown miner s.n.* (HOLOTYPE: catalogue number Sd-9-27B, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Flower pistillate, total length 4.5 mm; calyx abaxially strigillose, 0.8 mm long, shallowly cup-shaped, with distinct, broadly acute lobes 0.45 mm long (Fig. 2), petals 5, free, valvate, lanceolate, acute, with incurved tip, spreading to revolute, 3.4 mm long, 1.5 mm wide, adaxial surface densely low-papillate, abaxial surface strigillose, filament tube cyathiform, glabrous, 1.8 mm long, 3.3 mm wide (Fig. 1), anthers 10, sterile, sessile, lanceolate, glabrous, 0.7–0.9 mm long, anther sacs narrow, indehiscent [or dehisced and empty on some anthers, (Fig. 1)], rim of filament tube with acute lobes between anthers, placement of anthers alternating slightly higher and lower, pistil present, style equaling anther tube in length, stigma capitate, minutely papillose, ovary strigillose.

Etymology.—from the Latin "glaesarius," of amber.

Trichilia antiqua K.L. Chambers, Poinar, & A.E. Brown, sp. nov. (**Figs. 3–5**). TYPE: HISPANIOLA. DOMINICAN REPUBLIC: amber mine in the northern mountain range (Cordillera Septentrional), 1995, *unknown amber miner s.n.* (HOLOTYPE: catalogue number Sd-9-27A, deposited in the Poinar amber collection maintained at Oregon State University, Corvallis, Oregon 97331, U.S.A.).

Functional gender of flower uncertain, total length 3.4 mm; calyx glabrous, rotate, ca. 0.8 mm long (Fig. 4), no lobes evident, remaining petals 5 of 6, free, valvate, lanceolate, acute, strongly recurved, 2.6 mm long, 0.7 mm wide, adaxial and abaxial surfaces densely low-papillate, filament tube cylindrical, glabrous, 1.8 mm long, 1.6 mm wide (Fig. 3), remaining anther 1 of 10, sterile, glabrous, subsessile, globose, diameter 0.47 mm (Fig. 5), rim of filament tube with acuminate lobes 0.4 mm long alternating with basal stubs of 9 missing anthers, alternate anthers positioned lower on the rim (Fig. 3), pistil apparently damaged due to insect predation.

Etymology.—from the Latin "antiquus," old.

DISCUSSION

The two species, perhaps contemporaneous in the same Mid-Tertiary amber deposit on Hispaniola, are distinguishable by several floral characteristics. Differences are seen in the pubescence of the abaxial surfaces of the calyx and petals, in the shape and lobing of the calyces, and in the shape of the filament tubes and depth of placement of the lower versus higher anthers on the rim. Minor differences are the incurved petal tips in *Trichilia glaesaria*, which seem not to be as prominent in *T. antiqua*, the sessile anthers of the first species versus the short remaining filament in the second (Fig. 5), and the acute versus acuminate lobes of the staminal tube (Figs. 1, 3).

As previously indicated, the flower of *Trichilia antiqua* shows damage to its reproductive organs, which we believe may be due to an insect feeding inside the filament tube on the pistil, devouring most of the anthers, and removing one petal. The single small and malformed anther on the holotype seems to be a developmental abnormality, rather than the result of insect damage. The ovary of a partly damaged pistil can be seen well down in the filament tube. The absence of normal anthers and pistil prevent us from assigning a gender to this flower. The perianth parts, filament tubes, and anther arrangement of both fossils favor their chosen assignment to *Trichilia*. The alternation of sharply pointed lobes with the sessile or subsessile anthers on the rim of the staminal tube in both species is characteristic of many neotropical taxa of this genus (Pennington & Styles 1975, Pennington et al. 1981). Also, the placement of the anthers in higher and lower positions on the rim of the tube is found in some *Trichilia* species, for example *T. appendiculata* (Triana and Planch.) C. DC. and *T. magnifoliola* Pennington (Pennington et al. 1981). Adaxially papillose petals are found in *T. glabra* L., *T. claussenii* C. DC., *T. pallida* Swartz, and *T. pittieri* C. DC., among others, while abaxially strigillose calyx, petals, and ovary are common in New World species of the genus (Pennington et al. 1981).

Due to the Mid-Tertiary age of the two holotypes, and to the lack of information on critical features of their vegetative habit and male flowers, we favor their description as novel species rather than proposing an

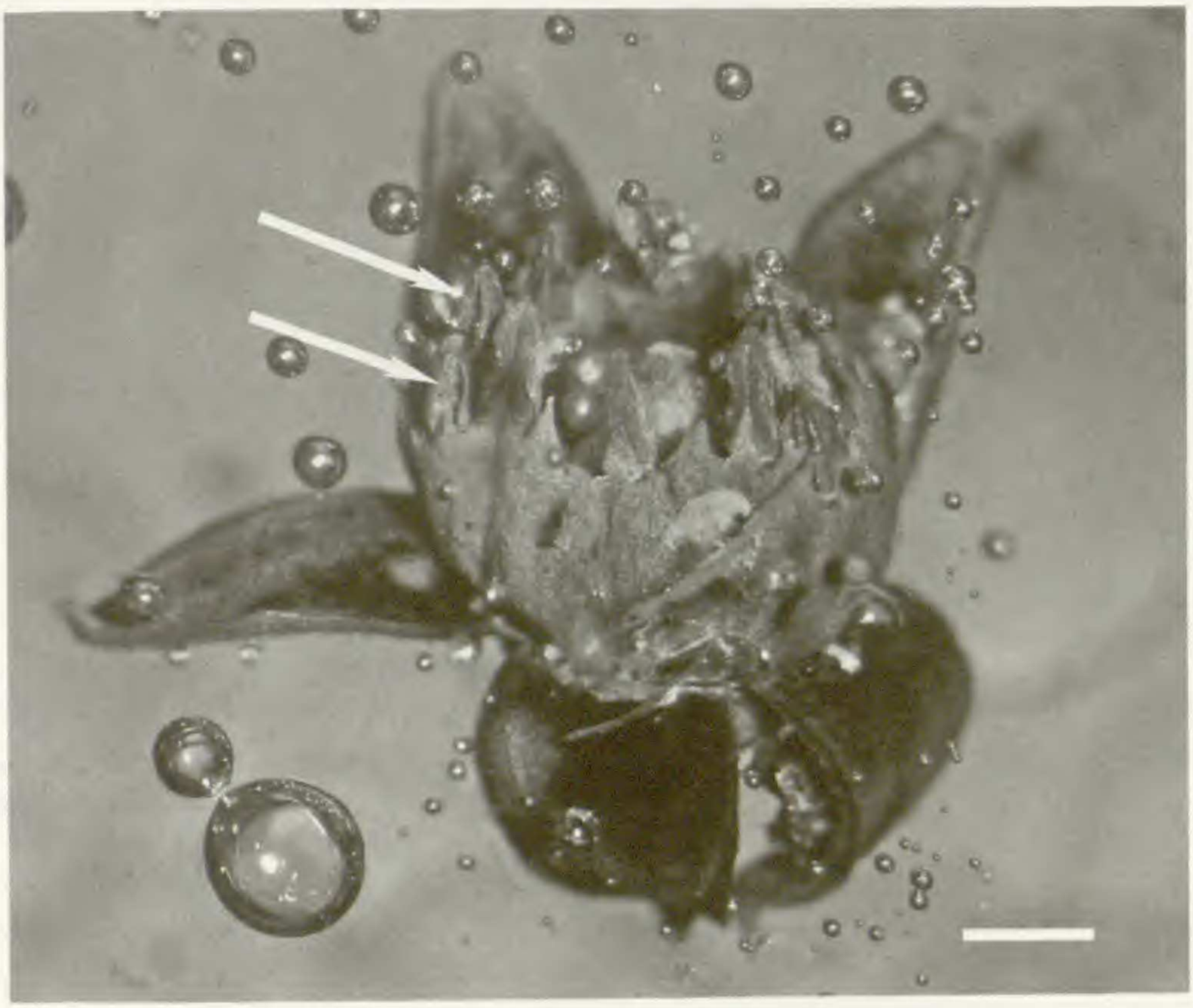

FIG. 1. *Trichilia glaesaria*. Flower in lateral view, showing alternating anthers and acute lobes on rim of filament tube. Note incurved tip of petal and capitate stigma visible within filament tube. Arrows indicate dehisced, empty anther sacs. Bar = 0.8 mm.

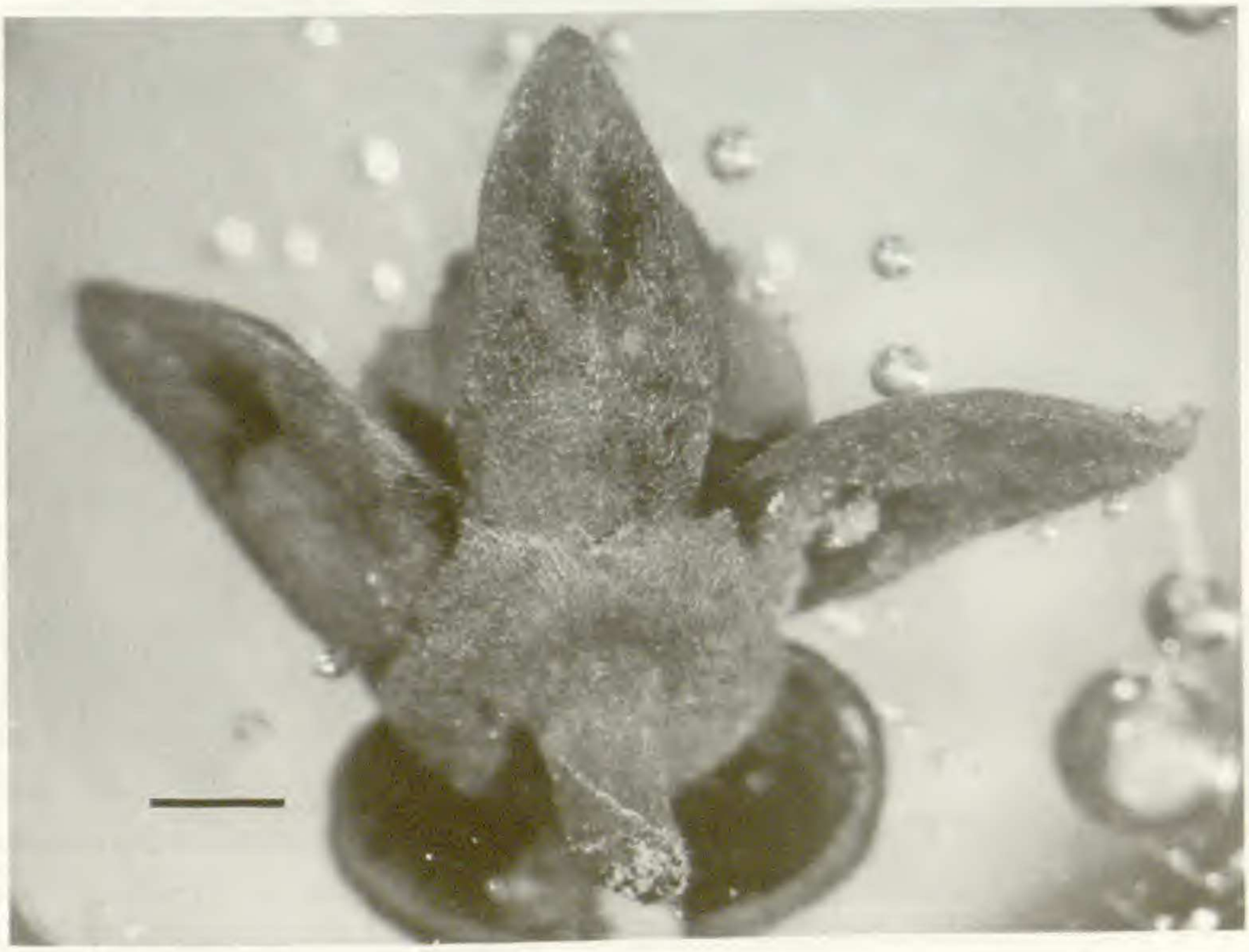

FIG. 2. *Trichilia glaesaria*. Basal view of flower, showing shallowly lobed calyx and abaxially strigillose petals and calyx. Bar = 0.8 mm.

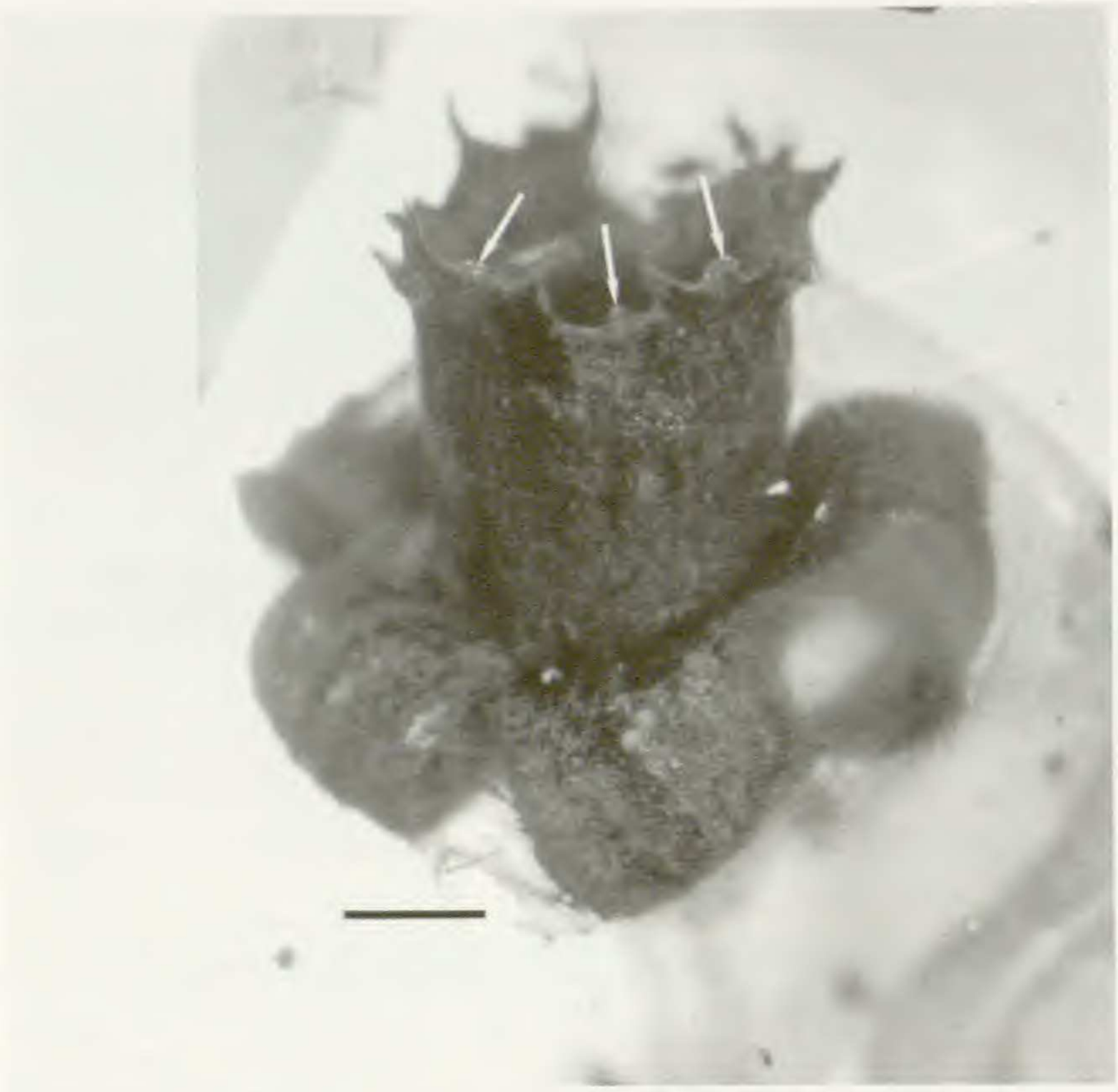

FIG. 3. *Trichilia antiqua*. Flower in lateral view. Arrows indicate basal stubs of missing anthers alternating with acuminate lobes at two heights on rim of filament tube. Bar = 0.6 mm.

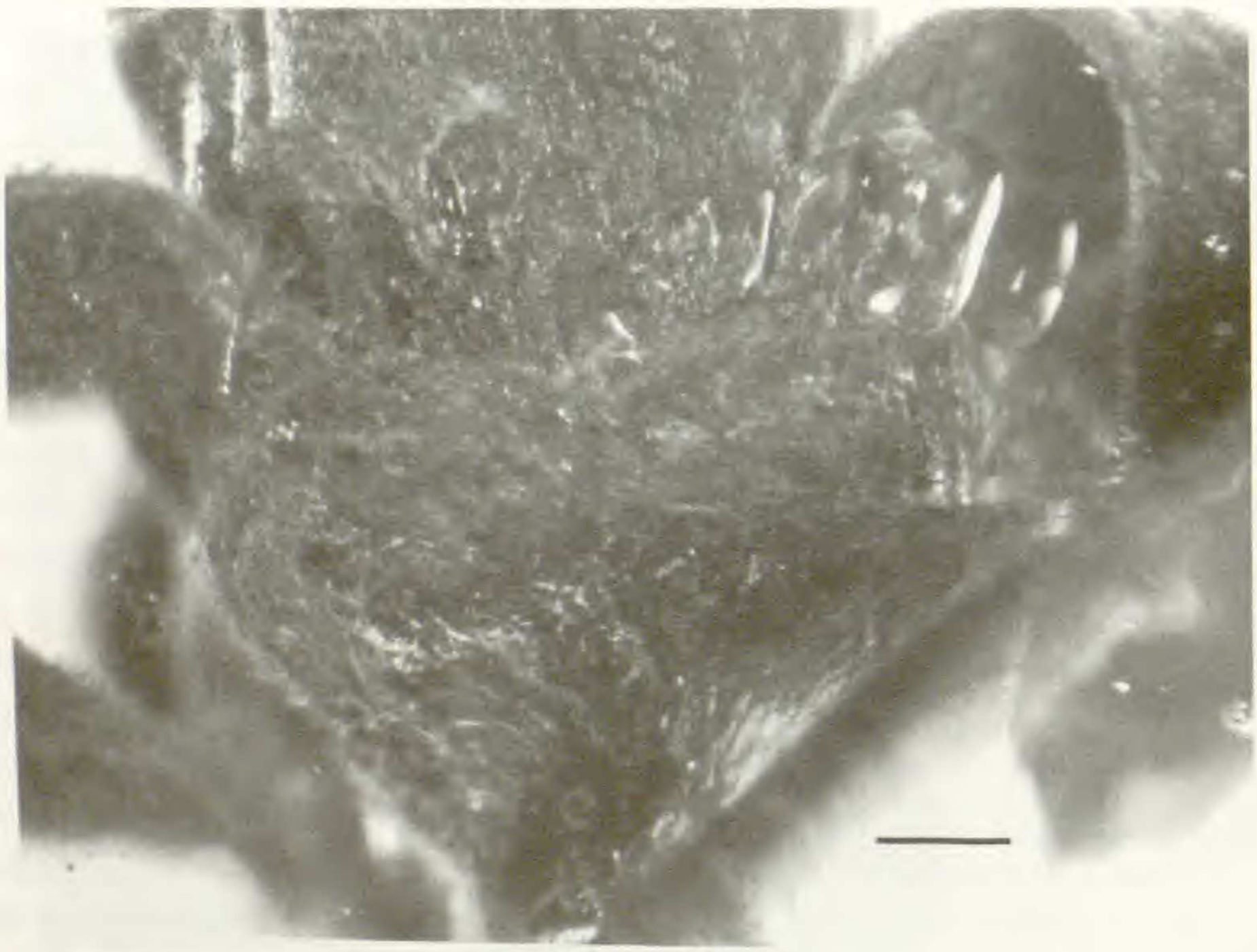

FIG. 4. *Trichilia antiqua*. Lateral view of base of flower, with rotate, glabrous calyx and scar of missing petal. Bar = 0.2 mm.

FIG. 5. *Trichilia antiqua*. Apical view of flower, showing rim of filament tube with remnant of abnormally developed anther. Anther tube obscured by debris from possible insect herbivore. Bar = 0.6 mm.

uncertain placement in particular extant species of this large and diverse genus (Pennington & Styles 1975). The critical differences between the two fossils are in the shape and pubescence of the calyx and the abaxial pubescence of the corolla. The relatively cup-shaped staminal tube of *T. glaesaria* versus the cylindrical one of *T. antiqua* might suggest only intraspecific variability, as for example in the difference between staminate and pistillate flowers in *T. moschata* Swartz, as illustrated by Pennington et al. (1981, p. 194). Variation in calyx shape and pubescence also occurs in some modern species, e.g. *T. schomburgkii* C. DC. (Pennington et al. 1981, pp. 162–167), in which the calyx may be "patelliform with 4–5 broadly ovate or triangular lobes...or [the] margin ± truncate, sparsely minutely puberulous or glabrate." As we have only the two examples at hand and cannot examine species variability, we have chosen to describe them as separate taxa, hoping this will assist in their comparison with modern species of Central and South America.

The fossil record of *Trichilia* is limited to a report from the Lower Miocene palynoflora of Cameroon ascribed to this genus (Salard-Cheboldaeff 1978, pollen named as *Psilastephanocolporites* [sic!] *grandis* n. sp.). In a paper by Muellner et al. (2006), this and other Meliaceae fossils, together with chloroplast DNA data, are the basis for estimates of divergence times in the family. The *rbcL* DNA cladogram presented by these authors includes a monophyletic clade of *Trichilia* and 11 other genera, which is assigned an origin in the Oligocene. Apart from *Trichilia*, members of this clade are presently limited to the Old World tropics, from Africa to Madagascar, India, Indo-China, Malesia, and Austroasia. Muellner et al. (2006) propose a West Gondwanan Cretaceous origin for the Meliaceae, with dispersal across Eurasia and between Eurasia and North America provided by the Beringian and North Atlantic land bridges, thence extending from North to South America via island chains or direct land connections during the Tertiary (cf. Muellner et al. 2010, with a dense sampling of Cedreleae). The age of the Dominican fossils is commensurate with the Oligocene crown age of the clade comprising *Trichilia* and relatives (Muellner et al. 2006). Concerning the crown group age of the modern genus *Trichilia*, however, the chronograms of Muellner et al. (2006, 2007) suggest a Miocene origin.

The placement of *Trichilia* in subfamily Melioideae (Harms 1940) has been confirmed by the DNA phylogenetic research (Muellner et al. 2003, 2007, 2008). However, the tribe Trichilieae, based on this genus, was resolved as non-monophyletic in the latter study (Muellner et al. 2008). Although Harms (1940) had divided *Trichilia* into 10 sections, only 5 of these comprise the genus in its modern circumscription, according to Pennington et al. (1981), and these authors go further in reducing the recognized sections to only two: Sect. *Trichilia* and Sect. *Moschoxylum* C. DC. Within *Trichilia*, the new species belong to the emended Sect. *Moschoxylum*, the defining traits being the valvate petals and completely united filaments.

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REFERENCES

CHAMBERS, K.L. AND G.O. POINAR, JR. 2010. The Dominican amber fossil *Lasiambix* (Fabaceae: Caesalpinioideae?) is a *Licania* (Chrysobalanaceae). J. Bot. Res. Inst. Texas 4:217–218.

CHAMBERS, K.L., G.O. POINAR, JR., AND A.E. BROWN. 2011. A fossil flower of *Persea* (Lauraceae) in Tertiary Dominican amber. J. Bot. Res. Inst. Texas 5:457–462.

DRAPER, G., P. MANN, AND J.F. LEWIS. 1994. Hispaniola. In: S. Donovan and T.A. Jackson, eds. Caribbean geology: an introduction. The University of the West Indies Publishers' Association, Kingston, Jamaica. Pp. 129–150.

HARMS, H. 1940. Meliaceae. In: H. Harms and J. Mattfeld, eds. Die natürlichen Pflanzenfamilien 19bl. Verlag Wilhelm Engelmann, Leipzig, pp. 1–172.

ITURRALDE-VINENT, M.A. AND R.D.E. MACPHEE. 1966. Age and paleogeographic origin of Dominican amber. Science 273:1850–1852.

MUELLNER, A.N., R. SAMUEL, S.A. JOHNSON, M. CHEEK, T.D. PENNINGTON, AND M.W. CHASE. 2003. Molecular phylogenetics of Meliaceae (Sapindales) based on nuclear and plastid DNA sequences. Amer. J. Bot. 90:471–480.

MUELLNER, A.N., V. SAVOLAINEN, R. SAMUEL, AND M.W. CHASE. 2006. The mahogany family "out-of-Africa": divergence time estimation, global biogeographic patterns inferred from plastid *rbcL* DNA sequences, extant, and fossil distribution of diversity. Molec. Phylogen. Evol. 40:236–250.

MUELLNER, A.N., D.D. VASSILIADES, AND S.S. RENNER. 2007. Placing Biebersteiniaceae, a herbaceous clade of Sapindales, in a temporal and geographic context. Pl. Syst. Evol. 266:233–252.

MUELLNER, A.N., R. SAMUEL, M.W. CHASE, A. COLEMAN, AND T.F. STUESSY. 2008. An evaluation of tribes and generic relationships in Melioideae (Meliaceae) based on nuclear ITS ribosomal DNA. Taxon 57:98–108.

MUELLNER, A.N., T.D. PENNINGTON, A.V. KOECKE, AND S.S. RENNER. 2010. Biogeography of *Cedrela* (Meliaceae, Sapindales) in Central and South America. Amer. J. Bot. 97:511–518.

PENNINGTON, T.D., AND B.T. STYLES. 1975. A generic monograph of the Meliaceae. Blumea 22:419–540.

PENNINGTON, T.D., B.T. STYLES, AND D.A.H. TAYLOR. 1981. Meliaceae. Fl. Neotropica 28:1–470.

POINAR, G.O., JR. AND R. POINAR. 1999. The amber forest. Princeton University Press, Princeton, NJ.

POINAR, G.O., JR., K.L. CHAMBERS, AND A.E. BROWN. 2008a. *Lasiambix dominicensis* gen. and sp. nov., a eudicot flower in Dominican amber showing affinities with Fabaceae subfamily Caesalpinioideae. J. Bot. Res. Inst. Texas 2:463–471.

POINAR, G.O., JR., K.L. CHAMBERS, AND A.E. BROWN. 2008b. *Trochanthera lepidota* gen. and sp. nov., a fossil angiosperm inflorescence in Dominican amber. J. Bot. Inst. Texas 2:1167–1173.

SALARD-CHEBOLDAEFF, M. 1978. Sur la palynoflore Maestrichtienne et Tertiaire du basin sédimentaire littoral du Cameroun. Pollen and Spores 20:215–260.

SCHLEE, D. 1999. Das Bernstein-Kabinett. Stuttgarter Beitr. Naturk. Ser. C, 28.